The Journal of HEREDITY

SNOWBALL COTTON RATS
(SEE PAGE 252)

Sterilization in Sweden

Dominance-Reversal in Cucurbita Colors

Computing Inbreeding Coefficients

Introgressive Hybridization

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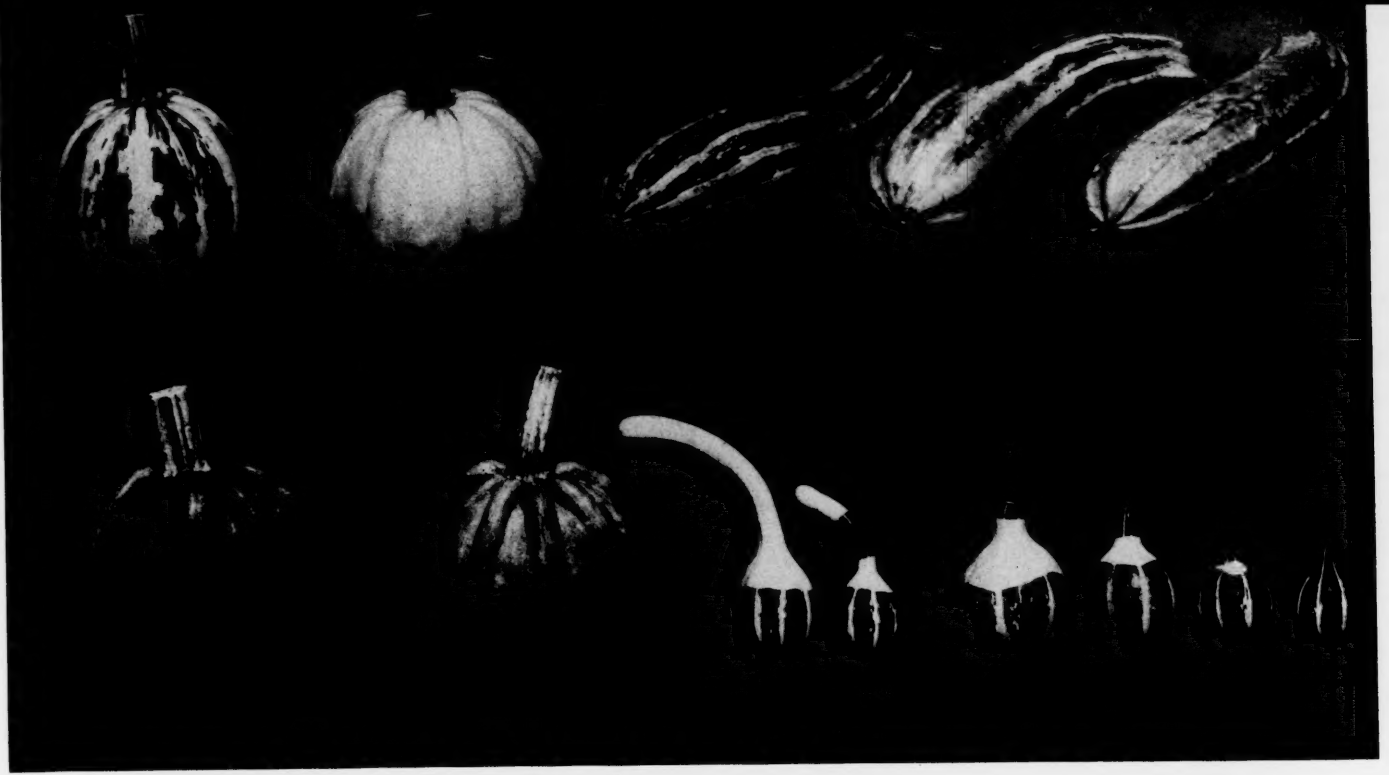

COLOR PATTERNS OF CUCURBITS

Figure 1

A—Two fruits of a primitive Mexican pumpkin taken from the same plant. The striped fruit on the left is mature, the other is uniformly dull white (tinged with pale yellow) at the "after ripening" stage. *B*—Showing changes in color and pattern from maturity to "after ripening" stage. In the squash variety Cocozelle, a conspicuous striping pattern of blackish green and yellow bands is visible at maturity. This is shown in the fruit at the left. After ripening, the fruit becomes a uniformly deep yellow. *C*—Gray fruits of primitive pumpkins from Mexico. Left, a fruit with blackish green stripes and gray ground color. Right, a fruit uniformly gray in color. *D*—Fruit variability on the same plant in the gourds. The two fruits on the left were harvested from a plant of the variety Spoon. The fruit on the extreme left is the more common type. The four fruits on the right were harvested from a plant of the variety Pear-Shaped Bicolor. The fourth from the right is the most common fruit for this particular plant, the other three being of less frequent occurrence. The cause of this type of variability is not known. The differences in age or size of fruits in this photograph have no bearing on color pattern.

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A DEVELOPMENTAL APPROACH TO THE GENETICS OF FRUIT COLOR

In Cucurbita Pepo L.

OVED SHIFRISS*

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THE species *Cucurbita pepo* L. represents a remarkable diversity of types in respect to fruit size, shape, and color. To this species belong the horticultural varieties of vegetable marrows, pumpkins, the "summer squash" of commerce, the yellow-flowered ornamental gourds, and related wild and semi-cultivated forms. All of these diverse forms have the same chromosome number ($n = 20$), and all are fully inter-fertile.

The purpose of this paper is to describe the major fruit color groups in *Cucurbita pepo* L. and discuss their genetical basis as far as it can be ascertained from available data. The character of fruit color is viewed as a *developmental* rather than as an end product manifestation; it is conceived as a sequence of events, including changes in hue, in intensity of color and pattern, from anthesis until after ripening.

Review of Literature

Sinnott and Durham[6] made the first study of fruit color in *Cucurbita pepo* L. They noted three main color groups; the whites, the yellows, and the greens, each of which may also occur in different intensities. These three groups are differentiated by two basic genes W_1-w_1 (or W_2-w_2) and Y-y. White (W_1 or W_2) is epistatic to yellow (Y) and yellow is dominant over green (y). These workers found considerable variation in color intensity within each group and also presented some data on the inheritance of striping. They asserted that "a stripe is a region in the fruit where the dominant body color is inhibited in its expression and where the recessive color is thus able to manifest itself."

Whitaker[8] crossed a white fruited Nest Egg gourd with a field Pumpkin, Mammoth Tours, said to be of solid green color. The F_1 was white and the F_2 gave a ratio of 3 white to 1 green. These results suggest that the white gourd was of the genotype *WWyy* and the green pumpkin *wwyy*.

Description of Major Fruit Color Groups

An excellent description of the horticultural varieties of *Cucurbita pepo* L. was published by Tapley et al.[7] This work consists also of several good color plates. Many of the 61 varieties described by Tapley were grown and observed by the writer with the exception of the obsolete sorts. In addition, quite a few inbreds from these and other varieties were grown as well as samples of the yellow-flowered gourds and wild and primitive forms obtained from the Southwest and Mexico.

For convenience, in classifying fruit color, the stretch of time from anthesis until after ripening can be divided into four stages: 1. *anthesis*, at blooming time when pollination and fertilization take place; 2. the active stage of fruit *development* and growth; 3. the stage at which the fruit attains its maximum size and seed reaches *maturity*; and 4. *after ripening*. The stage "after ripening" requires further explanation. A given

*The writer wishes to express his thanks to Professor Edmond W. Sinnott for furnishing the gourd seed used in this investigation and for his valuable comments on an earlier version of the manuscript. The photographs which accompany this article are courtesy of the W. Atlee Burpee Company.

fruit may be considered "mature" or "ripe" in respect to fruit development and seed maturity without having reached the end-product color. Therefore, "after ripening" refers to the stage at which the fruit attains its final color and no further changes are observed.

Altogether more than 250 samples were under observation. On the basis of developmental color manifestation the following tentative classification of major fruit color groups is given:

Group I. *Persistent white*

Fruit color at anthesis is grass green, usually uniform or with inconspicuous lace-like pattern, turning abruptly into white and remains white throughout.

Typical representatives of this group are the White Nest gourds and certain inbreds of White Bush Scallop (see Figure 2, also color plate in Tapley[7] between pages 50 and 51) and Long Island Bush. Some cream fruited inbreds of the latter two varieties may be related genetically to this group or to group IX.

Group II. *Persistent greens*

To this group belong Pear Shaped and other similar yellow-flowered gourds which retain their green color for a long time, even in storage. These persistent greens, occasionally striped, are very distinct and never become blackish green as do the Zucchini varieties of group VII.

Group III. *Persistent grays*

Certain primitive pumpkins from Mexico are uniformly gray in color (Figure 1*C*). The gray is sufficiently different from the greens of group II to be recognized as a distinct category.

Group IV. *Persistent yellows* (BBC[1]* Saffron Yellow 7/2)

Immature fruits are pale cream, becoming pale yellow, and then yellow at maturity as well as after ripening. A typical representative of this group is the relatively new variety Early Prolific (not to be confused with Earliest Prolific of Tapley[7]).

Group V. *Persistent Orange* (BBC[1] Orange 12)

Fruit color at anthesis is sulfur yellow, changing into deeper yellow and then becoming orange at maturity and after ripening. Summer Crookneck (see color plate in Tapley[7] between pages 48 and 49), Summer Straightneck, Yellow Bush Scallop, etc.

Group VI. *Persistent bicolor pattern*

Fruit is conspicuously marked by a well-defined pattern of green and yellow areas, at all stages of development. In some inbreds the green area is around the apex and the yellow around the basal-end, the two areas have only one common joining line. In other inbreds, the green is at both ends of the fruit, the yellow area in between. The relative size of each color area may vary in different lines. Most of the bicolor fruits observed by the writer were also striped; pale green in the green area and pale yellow in the yellow area. Typical representatives of this group are Bicolor Pear, Bicolor Spoon and other similar yellow-flowered gourds.

A unique type of fruit color variability, *on the same plant*, was observed in this group. Occasionally, a plant may be found in the Bicolor Pear which bears incompletely as well as completely green fruits, in addition to the typical bicolor ones (Figure 1*D*). Also, a few plants can be found in the Bicolor Spoon which bear "ringed" fruits. The latter have a narrow green ring around the "handle" (Figure 1*D*). It is significant that the differentiation into completely green and completely bicolor fruits occurs at a very early stage of development, before anthesis.

The basic phenomenon of fruit variability, *on the same plant*, independent from strictly post developmental influences or environmental modifications, is not entirely uncommon in *Cucurbita pepo* L. It is a puzzling problem in physiological genetics.

Group VII. *Developmentally green but turning orange after maturity or during storage.*

Fruit at anthesis is grass green becoming blackish green at maturity. In the light-exposed surface of the fruit the change to orange occurs after maturity or in storage. This change may be rapid and complete in some varieties or fairly slow and incomplete in others. Partial darkness hastens this change in storage. In the field, the portion of the fruit facing the ground is white or whitish green during development but becomes orange at maturity. The early appearance of orange color in this portion is indicative of full seed maturity. On the basis of developmental history the group can be divided into two subgroups:

Subgroup A. Immature fruits are strictly green, obscurely spotted or have inconspicuous lace-like pattern. Black Zucchini and Burpee Fordhook Zucchini Improved (Figure 3*B*) are good representatives. These two varieties and their relatives may differ from each other in the speed of conversion from green to orange and in other minor respects.

Subgroup B. Fruit at anthesis is *uniformly* grass green, turning sea-foam green, grayish green, and finally blackish green at maturity as in Subgroup A. A typical representative is Table Queen (see color plate in Tapley[7], between pages 48 and 49).

Group VIII. *Developmentally distinct lace-like green pattern turning completely into*

*The references "BBC[1]" and "MP[3]" are to Literature Citations 1 and 3.

cream yellow, or orange on approaching maturity.

The fruit at anthesis and early stages is well marked by a lace-like green pattern on a light green or whitish green background. Occasionally, one can also see narrow longitudinal stripes of dark green color. The whole fruit becomes gradually darker green, sometimes almost uniformly dark green, and then, just before maturity, it turns quite abruptly into yellow or orange.

Subgroup A. *Yellow* (BBC[1] Saffron Yellow 7)

A typical representative is the English variety Tender and True.

Subgroup B. *Orange* (BBC[1] Tangerine Orange 9/1 or MP[3] 3 C 11)

To this subgroup belong Cheyenne Bush, Connecticut Field, Golden Oblong, and Small Sugar (see color plaes in Tapley[7] between pages 38-39 and 46-47). These varieties differ slightly from each other in time and speed of conversion from green to orange. Certain inbreds of Sandwich Island, Winter Luxury (see color plates in Tapley[7] between pages 46-47 and 50-51), and Tours may belong here.

Experimental data, which will be presented later on, suggest the existence of a third subgroup of cream color.

Group IX. *Developmentally inconspicuous lace-like green pattern fading into whitish green or nearly white, and then turning cream, yellow or orange.*

The fruits at anthesis are either spotted or have an inconspicuous lace-like green pattern on a whitish green background. They appear almost white at immature marketable stage, then turn cream before maturity and finally either stay cream or change into yellow or deep yellow (almost orange).

Commercial varieties of this group may be variable in their end-product color.

Subgroup A. *Cream*

Good representatives are a few inbreds of the variety English Vegetable Marrow (see color plate in Tapley[7] between pages 32 and 33). It is not quite certain whether Fordhook and Perfect Gem belong here.

Subgroup B. *Yellow*

Typical representatives are certain inbreds of Long White Trailing and similar English vegetable marrow varieties. The obscure lace-like light green pattern turns whitish green, MP[3] Sea-Foam Yellow 17 C 2, then MP[3] Chamois 11 I 5, and finally to MP[3] Brass 11 L 6 (or yellow cream to dull yellow depending on strain).

Subgroup C. *Deep Yellow* (BCC[1] Cadmium Orange 8)

To this subgroup belong certain inbreds of Moore's Cream and related varieties. The whitish green inconspicuous lace-like pattern changes into seafoam color, to MP[3] Amber Yellow 10 J 3, BCC[1] Cadmium Orange 8/1 and then to BCC[1] Cadmium Orange 8; final surface color is uniform, pattern lacking or too inconspicuous to be visible. The small fruited Warted and Orange Apple gourds may also belong here.

Group X. *Developmentally green striped turning gradually into either white, cream, or deep yellow.*

At anthesis and immature stages the fruit is distinctly marked by longitudinal alternate light and dark green stripes in an overall pattern of lace work and/or splashed irregularly with dark green blotches. On approaching maturity, the dark green stripes turn blackish green and the ground color changes into white, cream, or yellow, depending on strain or variety. The blackish green stripes of some varieties may not change completely into orange even after a long period in storage.

Subgroup A. *White*

The dark green stripes may persist for a long while or turn into pale yellow and then white, tinged with yellow. Typical representatives are samples obtained from Mexico and certain yellow-flowered gourds. Mandan (see color plate in Tapley et al[7] between pages 42 and 43) and other similar varieties may belong to this subgroup.

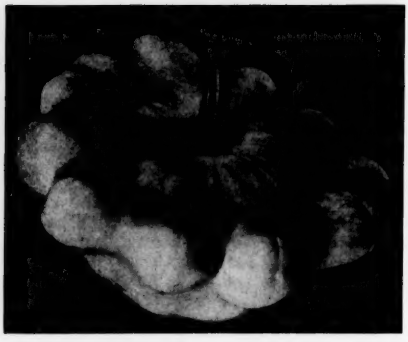
Subgroup B. *"Cream"*

This subgroup is quite unique. The cream ground color is different from the creams found in other groups. A typical representative is Delicata, also known as Sweet Potato (see Figure 3*A*). The blackish green stripes and the irregular dark green spots change into pale orange and the whole fruit eventually appears dark cream spotted with pale orange, in storage.

Subgroup C. *Deep Yellow*

At full maturity the dark green stripes become blackish green and the light green alternate stripes turn yellow. After maturity, in the field or in storage, the whole surface of the fruit turns into a uniform deep yellow color (see Figure 1*B*). Typical representatives are Italian Vegetable Marrow (see color plate in Tapley et al[7] between pages 42 and 43), Cocozelle, Improved Green Bush, Long Green Trailing, Table Dainty, etc.

Among the varieties of this group there is considerable variation in degree of regularity of the stripes and there is also variability in the pattern of the stripe itself. The stripe consists usually of dark green areas, arranged in a more or less continuous longitudinal band on a lighter green background. However, in a number of Mexican varieties the stripe is of a conspicuous mosaic pattern consisting of various shades of gray and green (see Figure 1*A*). After maturity, the light green shades turn yellow and the gray is fading later on into white. Thus, the pattern may have at least four different hues and shades of color.



PERSISTENT WHITE

Figure 2
A typical white fruit of the variety White Bush Scallop. This particular fruit has an inconspicuous lace-like pattern. Some white gourds are uniform white, devoid of any pattern (see Text Group I).

Miscellanea

A number of colors and patterns have not been classified yet. Among these are fruit colors of wild gourds of the Southwest and Mexico, belonging to *Cucurbita texana* and related forms or subspecies. The Texan gourd is very close taxonomically to the yellow-flowered ornamental gourds and may be regarded as the prototype of *C. pepo* L. The samples of the Texan gourd which the writer observed in trials are developmentally green or bluish green but never blackish green as in Group VII. The fruits are usually spotted with white and this pattern is particularly conspicuous on approaching maturity. In some forms the fruits turn into dull white after maturity and in others the green and white pattern is retained for a long while. These primitive fruit color types result perhaps from various combinations of genes for white color and green patterns.

Reversal of Dominance

The developmental approach to genetical analysis of color in the pumpkins was prompted by earlier work on reversal of dominance. It has been shown[5] that in crossing green and yellow fruited strains of the variety Table Queen the F_2 ratio *at anthesis* is 3 green to 1 yellow and *at maturity* 1 green to 3 yellow. This reversal in the genetical ratio is due to the response of the heterozygote which is green at early stages of development and yellow later on. If a given yellow variety is crossed with a number of different green varieties the resulting heterozygotes may differ from each other in stage at which the reversal begins as well as in its duration. In some heterozygotes the reversal is abrupt and takes place early in development whereas in others it may be slow and incomplete for a long while.

Reversal of dominance is not infrequent in crosses between various fruit colors and fruit color patterns in this species. In fact, there is ample evidence to indicate that the state of heterozygosity is one of the many causes for the fascinating variability in fruit color of the mixed ornamental gourds. For example, fruits that are bicolor at early stages and white or yellow later on are heterozygous whereas fruits that are persistently bicolor, green, or yellow are homozygous.

This phenomenon may be more universal than hitherto realized but one can hardly expect to be aware of it if a given character develops very rapidly towards its ultimate end-product manifestation, as many characters do. On the other hand, one is more likely to observe reversal of dominance in characters which express themselves during a relatively long period of time.

The relation between chromosome number and this phenomenon is also interesting. In Coleus, Rife[4] reported that diploid plants homozygous or heterozygous for *P* are of even purple color throughout development and the recessive *pp* individuals have special color pattern. However, when a tetraploid pattern *pppp* was crossed with a diploid even purple *PP*, the triploid offspring, evidently *Ppp* (or *Pppp*), "resembled pattern plants when quite small but gradually became purple and at maturity appeared as the purple parent." It is quite possible that this is a case of reversal of dominance in which at least two doses of the recessive are required against one

dose of the dominant gene to make the reversal visible.

The physiological aspects of reversal of dominance have been discussed by Goldschmidt.[2] It is fairly simple to interpret this phenomenon if character is conceived as a product of *rate* and *time* factors. In the cross between the green and yellow pumpkins, for example, one can assume that the heterozygote produces an intermediate rate of accumulation of carotinoids. Therefore, in this heterozygote, a longer period of time is required for the yellow color to become visible than in the yellow homozygote which is assumed to produce a relatively high rate of accumulation of carotinoids. Thus, *it is possible to have a complete dominance, in the orthodox sense, even though the gene in the heterozygous state produces strictly an intermediate action.* The theoretical implications of the reversal phenomenon, especially in regard to hybrid vigor, have been discussed previously by the writer.[5] It should be emphasized, however, that we actually know very little how the reversal is brought about. Nevertheless, the practical utilization of this phenomenon is quite clear. Here we have a new method in breeding for differentiating homozygotes from heterozygotes, both of which are otherwise indistinguishable phenotypically in their end products.

Additional Data on the Inheritance of Fruit Color

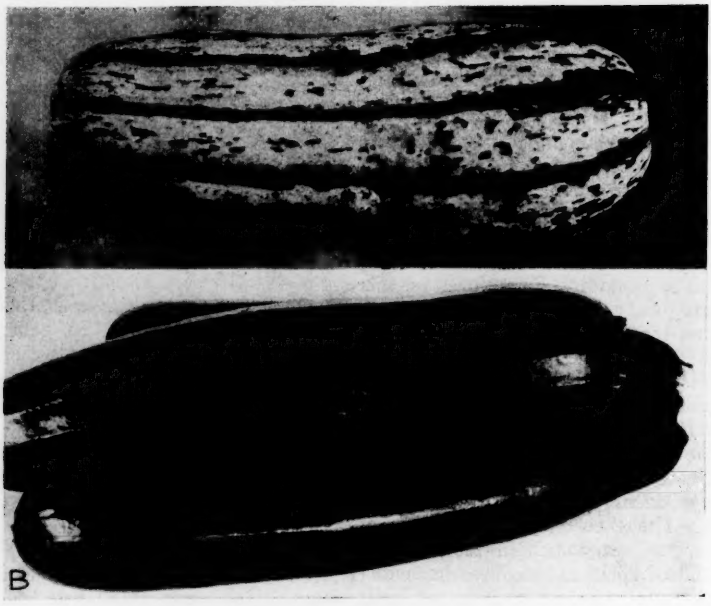
A cross was made between an inbred of the orange pumpkin Connecticut Field (Group VIII) and a white gourd (Group I) inbred of *Cucurbita pepo* var. ovifera. The fruit of Connecticut Field is a large flattened sphere averaging about twenty-five pounds or more and the gourd fruit is pear shaped, weighing about two ounces. At anthesis the pumpkin fruit has a lace-like green pattern on a lighter green background; during development the fruit becomes darker green and upon approaching full maturity it turns completely orange. In contrast, the gourd is *uniformly* green, at anthesis, abruptly changing into white and remaining white as long as the fruit can be kept in storage. The F_1 behaves as the gourd in being uniformly green at anthesis and then white. However, at maturity, the F_1 turns pale cream and becomes dark cream in storage. The description of the parents and the F_1 as well as the classification of the F_2 are presented in Table I. The F_2 data are based on *individual plant history.* The original number of the F_2 plants was 193 but the final classification was based on only 164 individuals. Some plants died during the season and others were too late in maturity. In general, the dark green fruited plants were considerably later than the whites.

The data in Table I show clearly that at anthesis the F_2 ratio is 3 uniform green to 1 lace-like green pattern. Later on in development all the uniformly green fruits turn white and all those of lace-like green pattern become darker green in color, resulting in a ratio of 3 white to 1 dark green of the lace-like pattern. Following this stage, the white fruited individuals turn cream, yellow (creamy yellow) or remain white and the green fruits turn cream (greenish cream), yellow (creamy yellow), and orange. It is necessary to emphasize that the creams and the yellows in this F_2 did not represent homogenous classes but varied considerably in intensity. This variability may be due partly to dose relationship in any given genotype as well as to other modifying factors, such as the number of pigmented layers in the skin, etc. The F_1 and most of the F_2 segregants resembled the gourd more than the pumpkin parent. The orange segregants had a gourd-like shell and their color was paler than the orange pumpkin.

The F_2 data of Table I are condensed in the following (overlook the pattern character for the moment):

Developmental Color Classification

127 white			37 green		
81	27	19	21	7	9
cream	white	yellow	cream	orange	yellow



STRIPES AND SOLID COLOR

Figure 3

A—The pumpkin variety Delicata has a distinct cream ground color unlike that of other cream in *Cucurbita pepo*. In storage, the fruit turns gradually into "orange." *B*—Typical fruits of the variety of Burpee's Fordhook Zucchini Improved (see Group IV in the text).

Classification of Final Colors

102 cream
27 white
28 yellow
7 orange

On the basis of the classification of final colors one is tempted to interpret the data as a dihybrid ratio: 102 (92.25) cream : 27 (30.75) white : 28 (30.75) yellow : 7 (10.25) orange, *P* between 0.50 to 0.30. However, if orange is differentiated by the double recessive genotype it would have been impossible for orange and white parents to produce an F_2 progeny such as above. There are of course other obvious reasons which make the dihybrid interpretation untenable. If we assume that the white gourd is of the genotype *WWyy* and the orange pumpkin as *wwYY*, to conform with the general scheme of previous workers, we should expect one-sixteenth of the F_2 population to be green, *wwyy*. However, such green plants have not been observed. Assuming the gourd is of the genotype *WWYY* and the pumpkin $wwY^{o}Y^{o}$ (Y^{o} orange dominant over *Y* yellow) it would still be difficult to explain the presence of a relatively large class of dark green fruits which turned cream or yellow. A more plausible interpretation, yet not conclusive, would be to assume that the white gourd is of the genotype *WWIIYY* and the orange pumpkin of the genotype $wwiiY^{o}Y^{o}$, *W* and *I* are genes with a differential inhibitory action on pigment accumulation. On the other hand, the alleles of gene *Y*, in this particular cross, control a complete developmental sequence with a turning point from green to yellow just before maturity. The F_1 would then be $WwIiY^{o}Y$ and the F_2:

27 *WIY*°—white changing to cream
9 *WIY* —white remaining white
9 *WiY*° —nearly white (seafoam) changing to yellow
3 *WiY* —nearly white (seafoam) changing to cream
9 *wIY*° —green changing to cream
3 *wIY* —green changing to pale cream
3 *wiY*° —green changing to orange
1 *wiY* —green changing to yellow

On the basis of this hypothesis the expected modified ratio of *final* colors is 42:9:10:3 and the data give a fairly good fit to this ratio: 102 (107.6250) cream:27 (23.0625) white:28 (25.625) yellow : 7 (7.6875) orange, *P* between 0.80 to 0.70. However, the data do not give a good fit to the expected modified ratio 30:9:9:12:3:1, based on *developmental* color classification. Considering the fact that the developmentally dark green class is relatively small the poor fit may not be a serious objection to the main thesis. An alternative hypothesis would be to assume that the pattern character, i.e. lace-like *vs.* uniform color distribution, hastens or slows down the development of pigmentation. However, the fact that 27 out of 37 green fruited individuals turned cream strongly suggests the presence of a partially inhibitory gene, in addition to the major *W* gene. It is quite likely that the pattern character is independent or incidental to the control of fruit color development. Moreover, gene *W* probably masked the expression of pattern segregants in the so-called uniform-green class (Table I).

According to our hypothesis, some creams and yellows are not basic colors but rather result from interaction between inhibitors and the gene for carotinoid accumulation. If this interpretation is correct, one would then expect to isolate from such a cross homozygous lines which are developmentally white (or nearly white) but which turn cream or yellow (*WWIIY*°*Y*°, *WWiiYY*, *WiiY*°*Y*°) as well as developmentally green races of the same final colors (*wwIIY*°*Y*°, *wwIIYY*). The survey of fruit color groups actually revealed the existence of such types among the horticultural varieties (Group IX and VIII), thus giving a substantial support to this hypothesis. The classification to nearly whites does not appear in Table I because the original data were gathered a few years before the complete survey was made and when our knowledge of various colors was rather meager. The writer believes that the distinction between whites and nearly whites could have been overlooked at that time. It appears, however, that the whites of Table I which turned cream or yellow are very similar developmentally to the English vegetable marrows. Indeed, the latter are known, in the trade, as whites—e.g. White Bush Marrow, because of their color at immature marketable stage.

The genetical mechanism which differentiates "greens" and "yellows" actually controls the biogenesis of chlorophylls and carotinoids and should be of particular interest from the standpoint of gene action. To begin with, the greens as a class cannot be regarded merely as residual heredity. Judging from their varied quality they result, in some cases at least, from the accumulation of chlorophyll by-products during the course of chlorophyll decomposition.

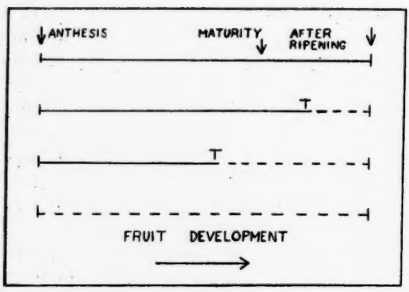
Figure 4 presents diagrammatically

TABLE I. Developmental analysis of the inheritance of fruit color in a cross between white gourd and orange pumpkin of *Cucurbita pepo* L.

Breeding Material	Color at Anthesis	No. of Plants	Color During Development	Color at Maturity*	No. of Plants
P_1 Pumpkin	Lace-like green pattern	....	Darker green, pattern conspicuous, changing to	Orange	....
P_2 Gourd	Uniform green	—	White remaining	White	....
F_1 ($P_1 \times P_2$)	Uniform green	—	White changing to	Cream	....
F_2	Uniform green†	129	White changing to	Cream	81
				White	27
				Yellow	19
				Unknown	5
	Lace-like green	42	Darker green, pattern conspicuous, changing to	Cream	21
				Orange	7
				Yellow	9
				Unknown	6
Total classified		171			164
Unknown		22	....	....	11
Grand Total		193			175

*Due to the marked difference in maturity between the parental lines and the relatively short growing season it is not quite certain that *all* the fruits were noted at exactly the same stage of maturity. The group of dark green color was generally later in maturity and its classification to final colors is subject to some modifications.

†Also includes, perhaps, fruits with inconspicuous lace-like green pattern.



COLOR CYCLE

Figure 4

Diagrammatic presentation of four major developmental differences between green and yellow fruited strains in *Cucurbita pepo* L. The length of time from anthesis to the after ripening stage varies from 40 days to over two months, depending on the strain. The solid line represents the developmental period during which the fruit is green, the dotted line, the yellow phase. *T* represents the turning point.

the developmental differences between various "greens" and "yellows." On the basis of available genetical data it is premature to assign certain genes for these characters. It is now clear, however, that the "greens" and the "yellows" differ not only in quality (gray, green, blackish green, yellow and orange) but also in their developmental manifestation. Besides persistent "greens" and persistent "yellows" there are developmentally intermediate types, each having a definite turning point, from the green to the yellow phase, just before or just after maturity. Is the rate of accumulation, or depletion, of chlorophyll by-products and carotinoids controlled by one or two independent genes? The data thus far accumulated strongly suggest that one series of alleles is involved.

Summary

The classification of fruit color groups in *Cucurbita pepo* L. and the discussion of their possible genetical control permit us to make a few general conclusions.

There are at least six different fruit colors in this species: *white, green, gray, cream, yellow* and *orange.* In addition, there is a series of patterns such as spotting, lace-like work, striping, and bicolor, each of which determines the design of color distribution on the surface of the fruit.

The six known colors are not static characters, as commonly conceived in genetical studies; they are related to a developmental sequence which has to be considered as a whole. To say that a given fruit is white or green or yellow is misleading unless the specific color is properly associated with a *stage* of fruit development. Of the ten major color groups described in this paper six are persistent, changing only in intensity, and four groups change in hue during development. The reaction of any given genotype can best be studied in terms of *rate* of pigment accumulation or depletion in relation to *time.* Regardless of whether fruits are similar or not in color at any given stage of their growth each genotype has a distinct developmental history of its own. There is a persistent white and another white which is confined only to early developmental stages. There are a few persistent greens as well as others which represent developmental phases, of different duration, which precede the expression of other colors. Moreover, some greens and yellows which are very similar at maturity or after maturity differ distinctly earlier in their history (Zucchini *vs.* Table Queen of Group VII; Moores Cream and Summer Crookneck of Groups IX and V). Here we have an unusual opportunity to identify genotypes by tracing the history of gene action through a relatively long period of time, for one month or over.

The practical implications of this analysis are obvious. In spite of our present incomplete knowledge of the genetics of fruit color, it is already possible to predict the breeding behavior of many phenotypes or to differentiate between homozygotes and heterozygotes (developmental reversal of dominance) by the use of a reference table which includes accurate developmental histories of known strains. Thus, it has been determined that most of the persistent color types, as well as some lines in other

groups, will always breed true upon selfing.

Finally, it should be emphasized that the remarkable diversity of fruit colors and patterns in this species and their interesting developmental manifestations present a challenging problem in physiological genetics.

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LAST OF THE SURVIVING MENDELLERS

George H. M. Lawrence
Bailey Hortorium, Cornell University

In the Journal of Heredity for March, 1949, Felix Kiefer contributed an important article on the last surviving discoverer of Mendel's Law, Erich von Tschermak, the other discoverers having been Correns and DeVries. There is no desire to dispute this history, but an American who led DeVries to the discovery of Mendel and who had cited Mendel as early as 1892 and who is now past his ninety-first anniversary is still actively engaged in his scientific work and botanical travel. I refer to L. H. Bailey, founder and director of the Bailey Hortorium at Cornell University.

Bailey[2] was the author of the term Plant-Breeding and in 1895 published a book on the subject. As early as 1892 he had published a pamphlet on *Cross-breeding and Hybridizing,*[1] in which was included a bibliography containing reference to Mendel. It was this reference that caused DeVries to look up Mendel. Bailey had early known DeVries and had gone to Amsterdam to see the OEnothera work from which came *Die Mutationstheorie* in 1901. DeVries had told Bailey that he had discovered Mendel by means of the Cross-breeding bibliography, and later wrote him a letter to that effect which, by permission, was published (p. 153) in a "new edition" of his book:[3] "I hope it will interest you to know that it was by means of your bibliography that I learnt . . . . of the existence of Mendel's papers, which are now coming to so high credit. Without your aid I fear I should not have found them at all." Bailey himself did not find access to Mendel's papers, but had read reference to them in European literature.

Tschermak was *privat dozent* in the University at Munich in Bailey's day and they had met. Only recently correspondence has passed between them.

In those days the great work of Mendel had not assumed the finality it now holds among many geneticists. Thus, John Coulter[4] in commenting on Bailey's *Plant-Breeding,* wrote: "It is a satisfaction that Professor Bailey has not been swept off his feet by the swelling tide of Mendelism. The wild prophecies that the application of Mendel's law will reduce plant breeding to a science of mathematical precision find him waiting for proof." (See also Rodgers,[7] p. 235.)

What is a Species?

Kiefer, in his article, spoke on the obtaining of "entirely new species" by "the artificial union of different types of plants." This raises again the old ques-

tion of the definition of a species. For two centuries and more most botanists have conceived of species in plants and animals as factual organisms recognizable by their evident morphology and perpetuating themselves in nature. If now the geneticist would define a species solely on the basis of its genetic constitution and behavior, on its chromosome number or other cytological characters, confusion is thrown into all the extensive taxonomic experience. The taxonomist is dubious about accepting chromosome number as a major criterion in the definition of a species. For one thing because ordinarily he is not able to identify or determine the character, and for another he knows that evidence exists[6] showing that chromosome numbers and characters do vary within elements recognized by geneticists as species. The geneticist in his initial studies is obliged to accept species as he finds them in the literature—and as proposed by the taxonomist—in order to make his records. He should be as critical of the determination of the taxonomic species with which he works as in the cytological features alleged to characterize species of presumed identity. We know that much of the genetic and cytologic tabulation current in the literature is unsound, because the names of the cited species have not been verified or authenticated. Further, no material is available by which later workers may make the necessary taxonomic analyses. These tabulations, particularly the compiled lists of chromosome numbers of species, will need to be reviewed as to their taxonomic accuracy before any careful taxonomist may accept them with confidence, and probably many of them will be discarded.

From all of this it is patent that the progress made during the period beginning 1892 has brought about fundamental changes in our views on speciation, for we know that species are more than subjective judgments and that to the contrary they are biological and phyletic elements. It must be recognized that the cytogeneticist has contributed much to our understanding of what is a species. Concomittant with this recognition is the knowledge that the species of the taxonomist is still an element based by necessity on morphological characters, and at the same time an element whose circumscription may be influenced, but not dictated by, valid data provided by the cytogeneticist.

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In re this matter of genetics and species, see also pages 256-7, where a *genetic* viewpoint is presented—Ed.

✦

A First Ad to Plant Hybridists

After having been punched, pierced, and prodded for a quarter of a century, and having reached the age when what previously was excellent eyesight must now be aided with glasses, we have as a result of this misfortune of years learned a new trick that may be of assistance to other plant hybridists.

Plant hybridists usually carry various small tools of their trade: tweezers, shears, needles, etc., on their persons when working at their profession. Usually these are carried in shirt or trouser pockets, often with decidedly uncomfortable results. After many years of suffering from painful punctures, the writer finally has learned that an ordinary metal eyeglass case is admirably suited for carrying the tools of the plant hybridist's trade. Although the open-end leather case will serve the same purpose. the writer prefers the closed metal case. A red one, if obtainable, is preferred as it is easily noticeable if dropped in the field, except in the red soil areas, where it may be worthwhile to paint the case with black and yellow stripes.

Frank A. Coffman

U. S. Department of Agriculture

STERILIZATION IN SWEDEN

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Department of Zoology, University of Uppsala

THE first Swedish sterilization law was passed in 1934 and was in force from 1935 to 1941. This law was considerably restricted. Voluntary sterilization during these years was to a great extent allowed without legal procedure. This principle, unique for Sweden, was no doubt somewhat hazardous but the number of such sterilizations was not great.

Grounds for Sterilization

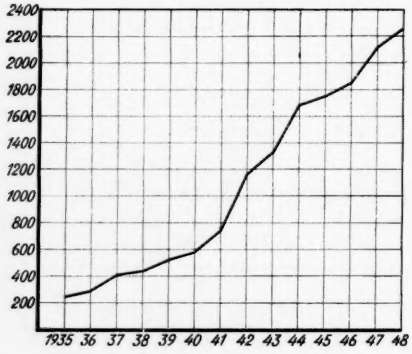
In 1941 a new law was enacted. This law sets forth three grounds for sterilization: one eugenic, one social, and one medical. According to the eugenic provision a person may be sterilized when there is reason to presume that mental disease, feeble-mindedness or severe disease or defect of another kind will be transmitted to his progeny. Sterilization on social grounds is allowed when a person, owing to mental disease, feeble-mindedness, or mental disturbance of another kind, or owing to an asocial manner of life, will be obviously unfit for taking care of children. The medical provision permits a woman to be sterilized if, owing to disease, physical defect or weakness, pregnancy would involve a severe risk for her life or health.

In principle, sterilization is voluntary. Yet persons who by reason of mental disturbance are unable to give legally valid consent to the operation because of "legal incapacity" in the eyes of the law, may be sterilized without their consent. This provision is especially important for the feeble-minded. Such "sterilization without consent," however, should not be confused with "compulsory sterilization" in the usual sense of the word. Sterilization may be decided upon, but the operation may not be carried out against the will of the person concerned; and physical constraint may not be used. Experience shows that almost all of the sterilizations approved are performed.

Sterilization on medical grounds, of women only, may take place after approval by two physicians. In cases of urgent abortion, the approval of only one physician is sufficient. In all other cases the operation must be approved by the Medical Board. The deciding board is a "social-psychiatric" council consisting of four persons specializing in the fields of general medicine, psychiatry, eugenics and women's social competency. Abortions and castrations may be approved by the same council.

There is an important connection between the law of sterilization and the Swedish law of abortion of 1938 to which subsequent amendments have been made, the most important being in 1946. When, for eugenic reasons on the side of the woman, abortion is decided on, this operation may, as a rule, be performed only on the condition that the woman is also sterilized. However, exceptions are made in special cases. An example is where sterilization seems superfluous owing to approaching climacteric or where it would imply a risk. This provision is an important part of the Swedish Abortion Law and has been of great practical value. When there is reason to prevent the birth of one child, because of the possibility of inheriting a severe defect from the mother, the woman should not be allowed to bear further children.

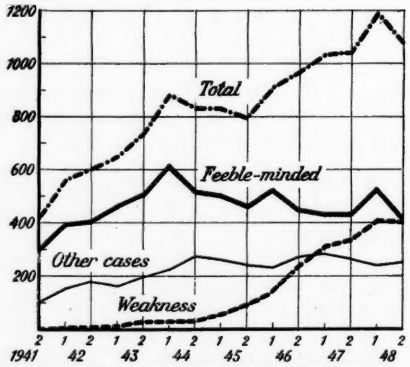
All sterilizations must be reported to the Medical Board. Of the three provisions cited in the law, often two or even three are present in a particular case. Thus where feeble-mindedness indicates sterilization there are usually strong eugenic reasons involved, since the average risk of producing oligophrenic children is at least 30 percent. Furthermore



STERILIZATION IN SWEDEN

Figure 5

The number of sterilizations reported in Sweden per year from 1935 to 1948. The original law was revised in 1941, with a consequent increase in number of sterilizations.



BASIS FOR STERILIZATION ANALYZED

Figure 6

Sterilizations per half year approved by the Swedish Medical Board from the adoption of the new Swedish Sterilization law in 1941. The revised law recognized three grounds for sterilization: eugenic, social and medical.

the feeble-minded are generally unfit to take care of children, and the social indication therefore is equally strong. As a matter of fact, the admission of social grounds of this nature is an enormous advantage even from the eugenic point of view. In cases where the hereditary nature of the defect seems uncertain but where the average risk of oligophrenic children is high, the social unfitness is obvious in most cases. Practically all feeble-minded below a certain level may thus be sterilized, which on the whole has a favorable eugenic effect. In psychoses there are often, in the case of women, both eugenic and medical reasons for sterilization. Frequently there are social reasons as well.

Frequency

The frequency of sterilizations reported from the year 1935, (when the first Swedish Sterilization Law was passed) to 1948 is shown in Figure 5. The differences between the numbers of operations reported and the number actually performed in the same year are comparatively small, except for the first year. There has been a steady increase from the very beginning, but the new law of 1941 has obviously caused an acceleration in this rise. In the last five years, 1944-1948, the number of reported sterilizations has been 1691, 1747, 1847, 2120, and 2261 respectively. 2200 sterilizations a year means about one in 3,000 or 0.032 percent of the population, including children and old people, and 1.7 percent of the annual births. A corresponding figure for the United States would be about 47,000 sterilizations a year.*

A total of 15,486 sterilizations (12,108 women; 3,378 men) was reported as performed in the fourteen years 1935 to 1948, according to reports received up to the end of February 1949. For the 7½ years between July 1941 and the end of 1948 the number is 12,533 (9,523

*In 1946 in the United States there were 1,476 sterilizations reported under the eugenic sterilization laws of 27 states. (*North Carolina Medical Journal*, Vol. 9, p. 75, 1948.) The highest rate for the feeble-minded was in Delaware, 10.2; and for the psychotic was in Virginia, 3.0 (*Publication No. 5*, Birthright, Inc., Princeton, N. J., 1947.) These, however, do not include sterilizations on social or therapeutic grounds. The recent years of Table I indicate about 14 per 100,000 for the annual sterilizations of the feeble-minded in Sweden and about 1.9 for those with psychoses. For the 27 states having sterilization laws the corresponding rates in 1946 were 1.8 and 0.8 per 100,000.—Ed.

women; 3,010 men.) These figures are too low, since a number of reports for 1947 and 1948 are not yet available. The final figures for the entire period will be approximately 15,650, and for the time covered by the new law about 12,700 sterilizations.

Analysis of the Material

In Table I the 12,569 cases in which sterilization was approved by the Medical Board are divided into seven groups according to the main indications.* The boundaries between the groups are not always sharp. The diagnosis of a case as psychosis or psychopathy may often be doubtful and a certain margin is left open to the subjective viewpoints of the psychiatrists who issue the medical certificate.

The feeble-minded include different grades, i.e., idiots (relatively few, many such being effectively segregated), imbeciles, and morons. The upper limit of mental age is about twelve years. I have not analyzed the material statistically from this point of view but I am under the impression that the mental age of most cases is between eight and a little more than eleven years. The decision of course is not solely based on the result of testing, which may be misleading, but also on a review of the general mental and social ability of the subject.

The category "eugenic reasons" embraces hereditary disease and defects. Some examples from the Swedish material may be given: several dominant abnormalities of eye, skin, and limbs, progressive muscular dystrophy, Huntington's chorea, Friedreich's ataxia, cerebellar ataxia, porphyrinuria (dominant), etc. In a number of cases sterilization has been approved (or, if abortion was applied for, prescribed) for a normal and healthy person because of the risk of the children getting a hereditary defect or disease, or where this risk at any rate was a predominant motive. Such cases include female carriers of hemophilia, and normal women or men (but the fathers are mostly more indifferent to this matter) who have already had a child suffering from obviously hereditary feeblemindedness or some other hereditary defect.

Under the heading of weakness, cases of psychically weak and worn out women are recorded. Most of these women are married, often with many children. The cases of physical diseases are few since they are not as a rule submitted to the Medical Board. The data of the table can be discussed better with the aid of incidence curves (Figures 6-8). In these diagrams the data are recorded for periods of half a year.

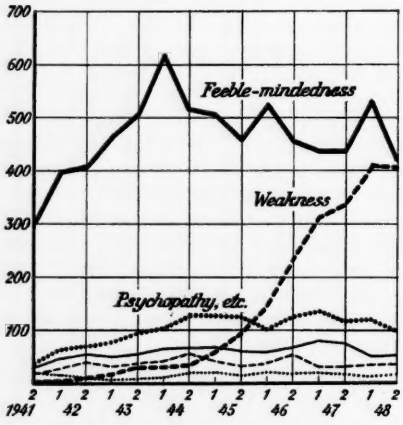
The total frequency curve (Figure 6) shows, as in Figure 5, a very marked and rather steep increase. The moderate decrease in the rate of sterilization of the feebleminded since 1943 may arise from the fact that the most obvious cases have already been dealt with.

The curve for weak and worn out women has risen to more than 400 in the last two half-years. This is undoubtedly due to the fact that the law and the new means of relief it offers to exhausted and often desperate mothers is gradually becoming more widely known. An important factor is the increase of legal abortions (Swedish law of 1938,

TABLE I. Sterilizations approved by the Swedish Medical Board, July 1941-December 1948.

	1941	1942	1943	1944	1945	1946	1947	1948	Total
Feeble-mindedness	305	810	978	1141	971	981	877	954	7017
Psychosis	30	103	106	134	129	128	157	109	896
Psychopothy, etc.	36	134	173	234	254	230	255	222	1538
Epilepsy	19	67	71	100	76	94	67	73	567
Eugenic reasons (only or mainly)	20	26	14	32	35	40	39	30	236
Feebleness (♀)	6	18	47	69	156	389	655	822	2162
Physical disease or defect (♀)	2	6	2	6	14	19	36	68	153
Total	418	1164	1391	1716	1635	1881	2086	2278	12569

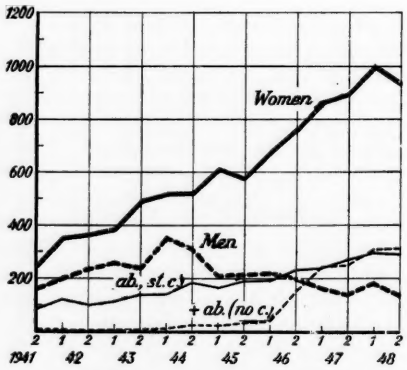
*In this and remaining tables and figures the numbers given refer, for practical reasons, to sterilizations approved by the Medical Board, a few of which may not have been actually performed. Sterilizations done on the approval of two physicians and not submitted to the Board have not been included.



ANALYSIS OF "OTHER CAUSES"

Figure 7

Number of sterilizations per half year approved by the Swedish Medical Board 1941-1948. The three lower, fine-line curves correspond to psychoses (continuous line), epilepsy (broken line), and (mainly) non-mental eugenic reasons (dotted line). "Weakness" is accepted as an indication for sterilization only in women.



STERILIZATIONS BY SEX

Figure 8

Sterilizations per half year approved by the Swedish Medical Board 1941-1948. The two fine-line curves show distribution of two special categories in cases involving women. The solid line (*ab., st.c.*) shows cases approved for abortion on condition that sterilization also be performed. The broken line (+ *ab. no c.*) represents cases where sterilization plus abortion is approved without making sterilization mandatory.

modified in 1946) since many worn out women applying for abortion wish to be spared further pregnancies.

The increase to be desired in the number of sterilizations of grave psychopathics of the unreliable and decidedly antisocial type is made difficult by the belief that this operation is a kind of castration or reduces the sexual capacity. Fear of the operation itself may also be a factor.

In Figure 8 the whole material (upper curve in Figure 6) is divided into men and women. The number of women is increasing, while that of men since 1944 has been decreasing. The number of feeble-minded men has diminished greatly. Figure 8 also shows the connection between sterilization and abortion. The curve for women who have obtained approval of abortion with the condition that sterilization be performed (feeble-minded, psychopathics, insane, and epileptics, if exogenous origin is not to be assumed, exclusively or essentially eugenic cases) shows a gradual rise. In several of these cases both operations were applied for but more often abortion alone. The curve for abortion plus sterilization in which the latter was not made a condition of approval (both operations applied for) shows a very steep rise in the second half of 1946. The cause is the marked increase of abortions on medical grounds, including weakness.

Risk of Death

Some words on the hazards of the operation should be added. For men, as is well known, the operation of vasectomy involves an extremely small risk, usually regarded as negligible. In adverse circumstances, however, the slightest wound may be disastrous. In 3006 cases (3374 if one begins with 1935) one death has occurred (a feebleminded man from septicepididymitis). For women salpingectomy involves the same general risk as other slight abdominal operations. Table II includes data on

sterilization of women under the new law (from July 1941 to the end of 1948).

The percentage of deaths in the whole material, 0.35 percent or one woman in 286, represents a maximum, and gives a false impression of the hazard of the operation in women who would be rated a good surgical risk. In these cases the risk is very slight. The material includes many cases in which any operation involved a greatly increased risk. Such cases are found mainly among the women operated after approval by two physicians because of physical disease. The deaths in these instances have been slightly more than one percent. These women suffered from more or less serious maladies: chronic nephritis, serious heart disease, pulmonary tuberculosis, sclerosis disseminata, abruptio placentae with serious hemorrhage, etc. The high percentage of deaths is thus easily explained.

The cases approved by the Medical Board show a much lower mortality of 0.21 percent or one woman in 470. The difference between the two groups is statistically significant (0.91 ± 0.28 percent). The figure for the Medical Board group, however, is also increased by cases of women in a poor state of physical health. If six such cases are excluded (a rough method, of course) the risk of deaths would fall to about 0.14 per cent or one in 700.

It is of interest to distinguish between simple sterilizations and such operations combined with abortion. Table III gives the data.

The difference which is statistically significant (0.42 ± 0.12 per cent) indicates that the risk is markedly greater when sterilization is combined with abortion. The cause is undoubtedly both the character of the operation and, presumably to a greater extent, the nature of the cases. This is shown by the second part of Table III.

Summary

A total of 15,486 sterilizations have been performed under Sweden's sterilization law passed in 1935 and expanded in 1941. Recently, there have been about 2,200 per year. For the United States the corresponding rate would be 47,000 annually.

The law provides for voluntary operation but sterilization of feebleminded may be decided without their consent. It recognizes eugenic, social and therapeutic grounds.

Sterilization is often combined with abortion for eugenic or therapeutic purposes.

There was one death in 3,374 vasectomies. For salpingectomy, the mortality was 1 in 286 cases when all cases of physical disease and emergency cases were included, and 1 in 470 when only 8,009 cases approved by the Medical Board were considered. For salpingectomy alone, performed on physically sound women, the mortality would be about 1 in 1,000.

TABLE II. Mortality in Sterilization Operations on Women Under the Swedish Law: July 1941-December 31, 1948.

	Number of operations	Deaths	
		No.	Percent
Approved by two physicians or in emergency cases by one physician	1429	16	1.12 ± 0.28
Approved by medical board	8009	17	0.21 ± 0.05
Total	9438	33	0.35 ± 0.06

TABLE III. Mortalities in Sterilization. Simple, or Combined with Caesarian Section or Abortion.*

	Number of women	Deaths	
		No.	Percent
A. With abortion or caesarian section	c. 4870	27	0.55 ± 0.11
B. Sterilization only	c. 4570	6	0.13 ± 0.05*
1. Two physicians and emergency cases with abortion or caesarian section	1020	15	1.47 ± 0.38
2. Two physicians and emergency cases, sterilization only	409	1	
3. Medical Board, emergency cases, sterilization with abortion or caesarian section	c. 3860	12	0.31 ± 0.09
4. Medical Board, sterilization only	c. 4150	5	0.12 ± 0.05

*The standard errors are calculated in the usual way. For the two groups, nearly coinciding, in which the incidence is only 6 and 5 respectively, a more complicated calculation ought to have been made. The skewness in the distribution, however, is not so great as to involve a serious error.

THE COMPUTATION OF INBREEDING COEFFICIENTS

For Closed Populations

DOROTHY CRUDEN
University of California, Berkeley

THE computation of inbreeding coefficients[2] for isolates of limited size is often a laborious procedure. When it involves path tracing in complicated pedigree networks extending over many generations it also contains many opportunities of committing errors. Approximate methods such as developed by Wright and McPhee[3] and empirically tested by Lush[1] may be of considerable value in many instances. There are undoubtedly many variations of these and other techniques which are in use in different laboratories, but by and large the published literature appears to be singularly lacking in computational instructions designed to relieve the tedium of path tracing and to ensure the accuracy of the computed values. The purpose of the present communication is to describe a method which to the writer's knowledge has not hitherto appeared in the literature. The particular features of this method permit the accumulation of data, so that the inbreeding coefficients for any generation may be directly determined from those obtained for preceding ones. Thus it eliminates the preparation and examination of long pedigree charts.

The method requires the computation of inbreeding coefficients of all possible matings and some hypothetical matings for a *single* (hereafter referred to as the base) generation early in the history of the line. The coefficients for later generations are then constructed as simple functions of the coefficients of the base generation. The formula for the coefficient of inbreeding developed by Wright[2] is a sum of distinct paths:

$$F_Z = \Sigma_A \ (\tfrac{1}{2})^{n_S + n_D + 1}(1 + F_A)$$

where A is an ancestor common to the pedigree of both sire and dam of Z, n_S is the number of generations between the sire and A, n_D is the number of generations between the dam and A, and F_A is the inbreeding coefficient of the ancestor A itself. It should be noted that this sum over the common ancestors can be taken in any order. This is pointed out because the method of computing F_Z here described is essentially no more than the specification of such an order.

The inbreeding coefficient will be obtained by this method for the pedigree shown in Figure 9 which contains a mating of parent and offspring, a mating of full-sibs, a mating of half-sibs and matings of more distantly related individuals. The individuals mated in generation I are unrelated except for j and k. The inbreeding coefficient obtained by tracing all distinct paths from X and Y, the sire and dam, respectively, of Z to each ancestor common to both X and Y is .11963.

It will be shown that the alternative method yields the same result without requiring that any paths be traced. It is based on the fact that *the inbreeding coefficient of the offspring of two parents is equal to the average inbreeding coefficient of offspring, perhaps hypothetical, from any one of the following sets of matings:*

(1) paternal parent mated with each of the two maternal grandparents;
(2) maternal parent mated with each of the two paternal grandparents;
(3) each of the two maternal grandparents with each of the paternal grandparents;
(4) each of the two maternal grandparents with each of the four pa-

ternal great grandparents, and so forth.

Thus, if we designate the coefficient of inbreeding which would have obtained for the progeny of any two animals *1* and *2* by f_{12},* F_Z is equal to any of the following expressions:

$$\frac{f_{XV} + f_{XW}}{2}$$

$$\frac{f_{YT} + f_{YU}}{2}$$

$$\frac{f_{TV} + f_{TW} + f_{UV} + f_{UW}}{4}, \text{ etc.}$$

It may be noted in the formulation presented that the actual sexes of the hypothetical parents need not be taken into account in using the coefficient f_{12}. Identical values may, for instance, result from the real mating of sire *1* to dam *2* and the presumed matings of dams *2* and *3* to each other if *3* is a full sister to *1 and neither 1 nor 3 appears in the pedigree of* 2.† In fact, self-fertilization, represented by f_{11}, may be assumed without prejudice to the technique.

We can verify the identity of F_Z as computed by the suggested method with the result previously obtained (.11963) if we consider the four f-values in the third of the expressions stated above,

$$F_Z = \frac{f_{TV} + f_{TW} + f_{UV} + f_{UW}}{4} =$$

$$\frac{.2969 + 0 + .01562 + .16600}{4} = .11963$$

These four values are obtained from Table III below. Table III is itself obtained directly from Table II and Table II directly from Table I.

Table I is computed as follows: for f_{12}, where *1* and *2* are two different individuals, we need only know the parents of each of the two. For example, $f_{ML} = (\frac{1}{2})^3 + (\frac{1}{2})^3 = (\frac{1}{2})^2$. F_1 is obviously = 0 except in the case of the individual denoted by *H* since all individuals in Generation I are known to be unrelated except *j* and *k*, the parents of *H*. The values along the diagonal, f_{11}, hypothetical self-fertilizations, are obtained from the column F_1, for $f_{11} = \frac{1}{2}(1 + F_1)$. This is simply the application of the Wright formula, stated previously, for the case in which n_S and $n_D = 0$.

TABLES I-III. Coefficients of Inbreeding in a closed population.

TABLE I.

		2	M	L	K	J	I	H	F	G	j	k
F_1	1	f_{12}										
0	M		.50	.25	0	0	0	0	0	0	0	0
0	L			.50	0	0	0	0	0	0	0	0
0	K				.50	.125	0	0	0	.125	0	0
0	J					.50	0	0	0	.125	0	0
0	I						.50	0	0	0	0	0
.125	H							.5625	.15625	0	.3125	.3125
0	F								.50	0	.25	.0625
0	G									.50	0	0
0	j										.50	.125
0	k											.50

TABLE II.

		2	Q	R	S	P	O	H
F_1	1	f_{12}						
.25	Q		.625	0	0	0	0	0
.125	R			.5625	0	.0625	0	0
0	S				.50	.03906	.2656	.2812
0	P					.50	.03906	.07812
0	O						.50	.2812
.125	H							.5625

TABLE III.

		2	T	U	V	W
F_1	1	f_{12}				
0	T		.50	.01562	.2969	0
.03906	U			.51953	.01562	.16600
0	V				.50	0
.2812	W					.6406

Then $F_X = f_{TU} = .01562$

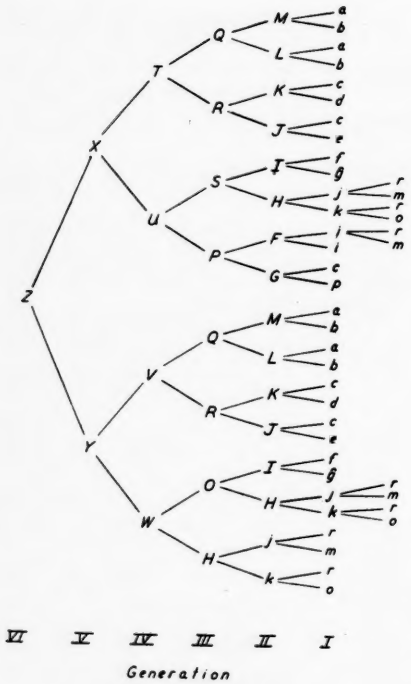
$F_Y = f_{VW} = 0$

and $F_Z = \dfrac{f_{TV} + f_{TW} + f_{UV} + f_{UW}}{4}$

$= .11963$

*Numbers will be used for general expressions to indicate any individuals, while letters will refer exclusively to individuals in the pedigree shown.

†When *both* 1 and 3 appear in the pedigree of 2 in the *same* generation this will also hold.



SAMPLE PEDIGREE

Figure 9

Pedigree of the example illustrated in the text. In Generation I, only individuals *j* and *k* are related.

The values of f_{12} in Table II are obtained by averaging the appropriate values from Table I. For example $f_{QR} = \frac{1}{4}(f_{MK} + f_{MJ} + f_{LK} + f_{LJ}) = 0$. Note that only the parents of *Q* and *R* need be known in order to compute f_{QR} directly from Table I. Similarly $f_{SO} = \frac{1}{4}(f_{II} + f_{IH} + f_{HI} + f_{HH}) = \frac{1}{4}(.50 + 0 + 0 + .5625) = .2656$. The values of F_1 are obtained directly from Table I since each F_1 in Table II is equal to some f_{12} in Table I; for example, $F_Q = f_{ML}$, $F_R = f_{KJ}$, etc. F_H is of course simply repeated since this individual was used both in Generation II and in Generation III. Again, the values along the diagonal in Table II, f_{11}, are computed directly from those in the F_1 column of Table II.

One point in the computation of Table II requires emphasis: a coefficient which represents, hypothetically, a self-fertilization cannot be expressed as an average of other coefficients. Thus to express f_{HH} as either $\frac{f_{Hj} + f_{Hk}}{2}$ or $\frac{f_{jj} + 2f_{jk} + f_{kk}}{4}$ would be incorrect since these averages actually represent f_{1H} where 1 is any full-sib of H. Clearly f_{HH} must be larger than f_{1H}. To find f_{OH} (or f_{SH}) for Table II then, from Table I we express f_{OH} (or f_{SH}) as $\frac{1}{2}(f_{IH} + f_{HH})$ and *not* as $\frac{1}{4}(f_{Ij} + f_{Ik} + f_{Hj} + f_{Hk})$. It will be observed, however, that $\frac{1}{2}(f_{IH} + f_{HH})$ can be expressed as $\frac{1}{2}(\frac{f_{Ij} + f_{Ik}}{2} + f_{HH}) = \frac{f_{Ij} + f_{Ik}}{4} + \frac{f_{HH}}{2}$.

The rationale of this method of constructing inbreeding coefficients can be understood by a closer examination of the component parts of any one of the averages by which F_Z can be represented. Consider the individual components of the particular representation of F_Z previously chosen:

$$F_Z = \frac{f_{TV} + f_{TW} + f_{UV} + f_{UW}}{4}$$

If each of the components is set up as a separate pedigree chart, it will be seen that the common ancestors of *T* and *V* for which distinct paths exist are *Q* and *R;* that there are no ancestors common to *T* and *W;* that the only common ancestor of *U* and *V* for which distinct paths through *U* and *V* exist is *c;* and that the common ancestors of *U* and *W* for which distinct paths through *U* and *W* exist are *I, H, j* and *r. Now the totality of common ancestors from these four separate matings, Q, R, c, I, H, j and r are exactly the set of ancestors common to X and Y, in the single pedigree for Z, for which distinct paths through X and Y exist.* Furthermore, it is obvious that the contribution of any one of these ancestors to a component, f_{12}, is $(\frac{1}{2})^2$ of the contribution of this same ancestor to $f_{XY} = F_Z$ because in the latter case we have included two

additional generations. For example, the contribution of Q to $f_{TV} = (\frac{1}{2})^3(1 + F_Q)$ while the contribution of Q to $f_{XY} = (\frac{1}{2})^5(1 + F_Q) = (\frac{1}{2})^2(\frac{1}{2})^3(1 + F_Q)$. Similarly the contributions of c to $f_{UV} = (\frac{1}{2})^7$, while the contribution of c to $f_{XY} = (\frac{1}{2})^9 = (\frac{1}{2})^2(\frac{1}{2})^7$. Thus

$$F_Z = f_{XY} = (\tfrac{1}{2})^2 f_{TV} + (\tfrac{1}{2})^2 f_{TW} + (\tfrac{1}{2})^2 f_{UV} + (\tfrac{1}{2})^2 f_{UW} = \frac{f_{TV} + f_{TW} + f_{UV} + f_{UW}}{4}$$

In general, the technique suggested calls for the computation of all possible combinations of matings between individuals of the base generation. In the pedigree illustrated the generation designated as II is taken as a base. However, the method can be used either from the inception of a line, as in the example given, or from a later stage when the line has been in existence for some time. In the latter case third or fourth generation progeny can be chosen as the base generation and a table like Table I set up for it. The f's are easily obtained for either of these generations since the pedigree for any particular individual will be very short and will be capable of repeated use in the various combinations. Attention should always be given to full-sibling relationships to avoid duplicate computations. Only one member of a full-sib family need appear in a table. Some sort of index of full-sibs is therefore helpful.

The principal advantage of the computation method here described is that it eliminates the use of pedigree charts, other than those required to compute all f's for the base generation, and thus reduces the likelihood of mechanical errors without in any way sacrificing the accuracy of the computation. Complete pedigree charts for inbred lines, going back seven or eight or more generations are virtually impossible to handle in a path tracing operation. The customary alternative of ignoring an arbitrary number of the earliest generations results in an underestimate of the true coefficient, particularly if the same individual appears in more than two generations.

A second advantage is to be found in the speed of computation. Since the data obtained for any one generation furnish the basis of calculation for each succeeding generation, the total time expended in calculating inbreeding coefficients for any given line is greatly reduced.

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LYSENKO'S BROTHER ESCAPES TO U. S.

THE *New York Times* of September 11 announced the arrival in the United States of industrial chemist Pavlo D. Lysenko, brother of Academician Trofim Lysenko, whose strange Marxist Genetics has recently been the subject of comment in this Journal. In an exclusive interview, Mr. Lysenko told a story all too frequently heard from refugees from the Soviet Union, of criticism, sabotage, and persecution. He is a specialist in coal chemistry, who between 1932 and 1942 was on the staff of the Institute of Coal Chemistry in Kharkov. In collaboration with his immediate superior, Platon Zarovny, Lysenko perfected a method of converting low grade coal into metallurgical coke. This invention ran afoul of party dicta, and in spite of successful tests, the final production was sabotaged at a critical time in the rearmament program. Zarovny's pledge to Stalin to produce large quantities of urgently needed toluene would have been met had he received the cooperation of his staff, Mr. Lysenko said. "But men under him sabotaged the program, even though they likewise sabotaged the defense of our country."

Zarovny was sentenced to three years in a prison camp, but through a change of administration the case against Lysenko collapsed. After many vissitudes, he was captured by the Germans. Later he was removed westward by the Germans when they retreated, and finally ended up in the American Zone in Munich. Fearing that he would be kidnapped and returned to Russia, he avoided calling attention to himself. In Germany, he set up an artificial honey plant, using inedible horse chestnuts as raw material. When he sold his make-shift factory to come to America he was employing four Germans.

In the annals of science, the story of the brothers Vavilov and of the brothers Lysenko may become something of a classic.—R. C.

SNOWBALL: A REPEATED MUTATION
In the Cotton Rat

C. H. DANFORTH AND VICTOR SCHWENTKER*

MOST spontaneous mutations occur unexpectedly and, as a consequence, the circumstances surrounding their appearances are often inadequately documented. Furthermore, after a mutation has once appeared, subsequent breeding experiments throw no further light on the nature of its origin. For this reason, as well as because of the recent revival of interest in factors influencing mutation in mammals, it seems desirable to record a spontaneous mutation in the cotton rat which has occurred twice within a period of about nine months. Because of its prevailingly white color, and to give it a distinctive designation, this mutant has been called "snowball" (Symbol *S*). The first one to appear (Figure 10 *A*) was born in the colony at Tumblebrook Farm, Brant Lake, New York, on January 21, 1947. A full record of it and its descendants has been kept by one of us (V.S.). The second mutant (Figure 10 *B*) was born on October 13, 1947, in the colony maintained by Mr. Ralph H. Martin, 882 Bell Street, East Palo Alto, California. The descendants of this mutant have also been followed with some care.

The cotton rat (*Sigmodon hispidus* Say and Ord.) is a relatively recent addition to the group of laboratory mammals, having been used extensively only during the last ten years.[1-7] There are several subspecies and geographical races, the most common one, in Southern United States, being *Sigmodon hispidus hispidus* from which all of our specimens are descended.

The original stock obtained by Tumblebrook Farm was captured in the wild near Montgomery, Alabama. Four males and three females left descendants. All of them and their offspring were of the characteristic agouti or "wild rat" color (Figure 10 *C*) and no mutations were noted prior to 1947. From 1943 to 1945 some 2,000 cotton rats from Tumblebrook Farm were sent to Dr. Hubert S. Loring of the Department of Biochemistry at Stanford for use in studies on the virus of poliomyelitis. Some of this stock was turned over to Mr. Martin, by whom it has since been maintained. The two substrains remained distinct from 1945 until after both mutations had occurred. During the war great numbers were sent from Tumblebrook Farm to England for manufacture of vaccine, and our records show that well over two million descendants of the original seven had been raised before the first mutation was observed.

Mutant A

The first mutant animal (*A*) was a female which appeared in a litter of seven, the rest of which were normal. This litter was the tenth of thirteen produced by the same pair of parents. Of their 95 young *A* alone deviated from normal. It was prevailingly white, but with small patches of agouti-colored hairs on the head and rump. The ears were dark, as was the tail except for its tip. All offspring of this pair from the tenth litter on were mated in brother-sister combinations, and all except the mutant produced exclusively normal young.

The mutant herself, mated to a brother from the same litter, produced between May 10, and December 20, 42 young in eight litters as follows: 1 normal (i.e., agouti-colored); 6 normal and 1 mutant; 5 normal and 2 mutants; 6 normal and 2 mutants; 3 normal and 1 mutant; 3 normal and 1 mutant; 4 nor-

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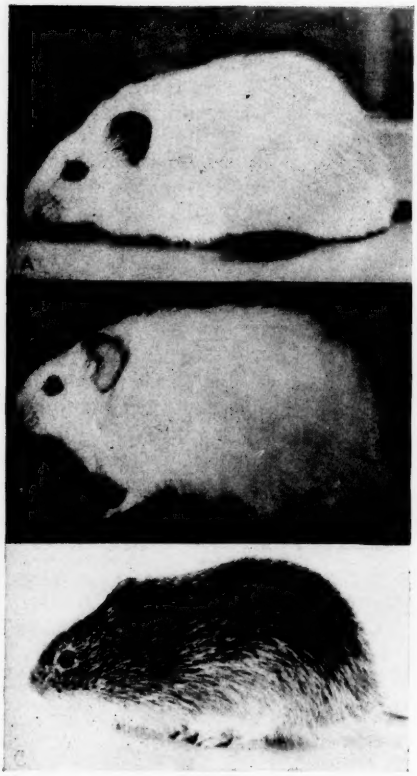

TWO MUTANT COTTON RATS COMPARED WITH NORMAL

Figure 10

A—The first mutant that appeared. This rat had pigmented eyes and a few agouti hairs on the head and rump (which, unfortunately, do not show in the photograph.) *B*—The second mutant rat. This animal had completely white pelage, but its eyes were fully pigmented and there was a slight amount of pigment in the ears and proximal part of the tail. *C*—An ordinary "agouti" or wild-type cotton rat. The two dominant white mutations appear to be identical.

mal and 1 mutant; 3 normal and 3 mutants—a total of 31 normal and 11 mutants. Of the latter, five were males and six were females. The mutants are easily recognized at birth, or even as late fetuses.

Mutant B

Mutant *B*, also a female, was very nearly pure white with only a slight trace of pigment in the skin of the ears and tail. As in Mutant *A*, her eyes were black, and dark eyes have been characteristic of all descendants of both females. Eyes from litter-mate normal and "snowball" prenatal young, when cleared and examined microscopically, showed no apparent differences in pigmentation.

For records of the immediate ancestry of Mutant *B* we are indebted to Mr. Martin. From his records it appears that the parents of Mutant *B*, a male 108 days old and a female of 106 days, were mated September 7, 1947. This pair produced 9 young on October 13; 6 on November 10; and one on January 23. One member of the first litter was mutant *B;* the rest were normal.

Mutant *B* was mated to a male which came from a sibship of 49. According to Mr. Martin, all of his rats up to this time with the sole exception of Mutant *B*, had shown only the typical wild type of coloration, and so have all subsequent animals except among those descended from *B*. Mutant *B* produced seven litters—one each in January, February, March, April, May, June, and August—with a total of 26 young, "about half of which" were of the mutant type.

Genetic Tests

By late spring, 1948, Mr. Martin had supplied a number of these mutant cotton rats to the departments of bacteriology and biochemistry at Stanford. Dr. Jane Anderson and Mrs. Nancy Lawrence of the latter department called them to the attention of one of us (C. H. D.) and supplied the Department of Anatomy with several specimens. Others were purchased from Mr. Martin, who also put his copious records at our disposal.

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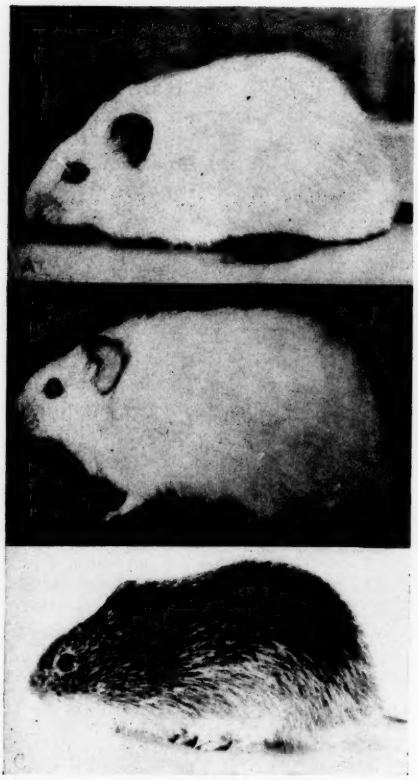

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Farm and from the Department of Anatomy at Stanford were exchanged for purposes of comparison and genetic checks. To all appearances the mutations are the same. Both Schwentker and Danforth had arrived independently at the conclusions that the mutant gene is dominant and probably lethal when homozygous. Thus far no mutant individual has been found to produce only mutant young. The fact that both *A* and *B* were females argues against sex-linkage, as does the distribution of sex among mutant as compared with normal young. Combining the Tumblebrook and Stanford figures, we have: from mutant × mutant, 189 mutant and 103 normal; from mutant × normal, 334 mutant and 337 normal—a very close agreement with expectations for a dominant gene which is lethal when homozygous. In crosses between the two lines it will take large numbers of offspring to differentiate between the 8/12 mutant young expected if the mutants are identical and the 9/12 expected if they were genetically different.

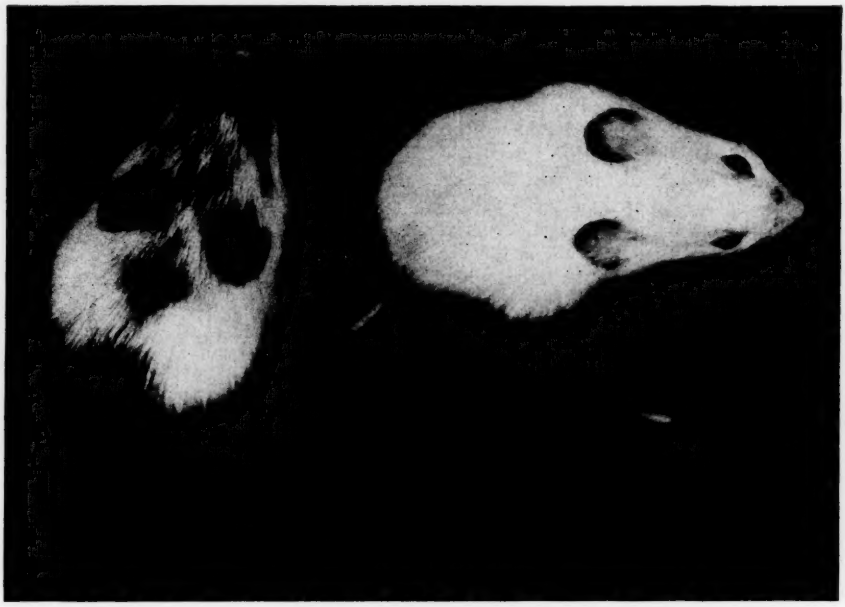
Although the susceptibility of the mutants to the Lansing strain of poliomyelitis has not been studied in fully controlled experiments, some data bearing on this question have been obtained by Professor Loring and his associates. In experiments in which tenfold serial dilution of virus was innoculated into different groups of rats containing one or more mutants, no difference in susceptibility to the Lansing strain was found between the mutants and normals. Several other laboratories are also cooperating in testing the relative susceptibilities of snowball and agouti rats to various pathogenic agents. As yet no differences have been found, but the former have an incidental advantage in their lighter color and more diversified patterns.

When Did the Mutations Occur?

The period in the life cycle during which the mutation producing this trait must have occurred can be placed within definite limits. It had to fall between the time in development of the parent and of the offspring when there ceases to be any cell which, in that individual, could have descendants in both the germ line and the neural crest. The neural crest is significant in this connection since according to Rawles[8] we must look to it as the source of all pigment in the pelage. If the mutation were to appear prior to the period in question, the *parent* would be the mutant; if later than this, the mutation would be either non-hereditary ("somatic") or non-apparent. Precisely when the critical limit is reached is as yet undetermined, but it must be subsequent to the first cleavage stage and presumably not much later than the formation of Hensen's node. If during this brief interval there is any moment at which there are several cells, the descendants of any of which may become either somatic or germinal, a mutation occurring at this time might be recognized as such, since it would tend to give either a somatic or a germinal mosaic. Our two mutants may be viewed in light of these considerations.

In the case of Mutant *B*, if Mr. Martin's impression that the young were about equally divided between mutant and normal is correct, there is every reason to suspect that the mutant gene either was present in one of the antecedent gametes or appeared so early after fertilization that cells of the entire germinal tract, as well as of the neural crest, were descended from the one cell in which the mutation originally occurred.

With Mutant *A* the evidence is different. Here the distribution of young deviates widely from expectation for a heterozygous parent—31:11 in place of 21:21, as expected. On pure chance, that much deviation in either direction would be expected not oftener than once in 390 times. The distributions in the several litters of this female are much closer to a 3:1 than to a 1:1 ratio. Assuming this 3:1 ratio, a 3:3 distribution such as appeared in the last litter, should occur about one time in eight.



SEGREGATION IN PROGENY

Figure 11

Litter mate young, representative of the three most common patterns. One of their parents was white; the other spotted.

In other words, the distribution of young in this case is such as might have been expected if the initial mutation had occurred at such a time in embryonic development that only about one-half, instead of all, the germ cells were descended from the original mutated cell.

Modifying Genes

While the two original mutant animals, *A* and *B*, differed slightly in the amount of white in their pelage, mated to normal males, each produced descendants that resembled the other. This presumably is due not to differences in the mutant genes themselves, but to a lack of complete homozygosity of other genes in the laboratory stock. Since some of the mutant animals have a considerable amount of typical agouti fur (up to nearly 50 percent in occasional representatives of both lines), it may be surmised that the gene for white is not an allele of the gene for agouti, but a modifier of it. The effect of the mutant gene itself is apparently limited in turn by other genes for which neither the New York nor the California stock is homozygous. If we designate the mutant gene as *S*, we must postulate at least one modifying gene, *M*, to account for variations in the amount of white. Thus far, among the descendants of *B*, pure white parents have produced young that were either almost or entirely white, or fully agouti. Pure white and spotted have given pure white, spotted, and agouti young (Figure 11). Finally, either pure white or spotted individuals mated to agoutis have produced all three types of young. Thus, a mutation in a member of one pair of alleles has quite incidentally brought to light the presence of at least one other pair which ordinarily would not have been detectible.

Summary

What appears to be the same mutation, a dominant white called "snowball" (*S*), has recently occurred in two different, but related, colonies of the cotton rat. In one case the mutation apparently took place in one of the participating gametes, or very shortly after fertilization; in the other, it may have occurred at an appreciably later period in the life cycle. The gene seems to be lethal when homozygous. Its exact expression is apparently contingent on the distibution of modifying factors which were already present in the parental stocks. One of these genes (*M*) makes the difference between an almost pure white pelage and a coat with an appreciable amount of agouti on the rump, shoulders, and head.

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INTROGRESSIVE HYBRIDIZATION

THIS first volume* in the Biological Research Series of John Wiley & Sons is an important contribution. But it is expensive at $3.00. It consists of pages ix plus 109. Of the ix, only the two-page foreword has anything to say. Of the 109, approximately twenty pages are figures, tables and blanks; four pages are bibliography; three pages are index. That leaves eighty-two pages of text. Of course, the author claims that "a good deal of what is presented . . . has never appeared in print." Perhaps so, but surely the ideas are familiar, and most of the figures. The bibliography is supposedly "limited to cited works." It is more limited than that: textual reference is made, for example, to two papers by R. J. Seibert, and only one appears in the bibliography.

The first chapter (pp. 1-11) reviews the well-known case of introgressive hybridization among Louisiana irises, as understood from the work of Anderson and others.

The second chapter (pp. 12-18) discusses the ecological basis of introgression: "It has been very generally recognized that if hybrids (in nature) are to survive we must have intermediate habitats for them. It has not been emphasized, however, that, if anything beyond the first hybrid generation is to pull through, we must have habitats not only that are intermediate but also that present all possible recombinations of the contrasting differences of the original habitats." One questions the accuracy of this last statement: such emphasis has been expressed.

The third chapter (pp. 19-48) reports the genetic basis of introgression. Operations of independent assortment and linkage are contrasted for hybrid generations. "The effects of linkage are greatly to increase the chances of getting F_2 recombinations very similar to the parental species and greatly to decrease the percentage of segregants more or less similar to the F_1." Character association is demonstrated to be a criterion of hybridity. Indeed Anderson states that a group of graduate students given mass collections of a hybrid population should

*Anderson, Edgar, *Introgressive Hybridization.* John Wiley & Sons, Inc. 1949.

be able to "draw up a technical description of the original hybridizing entities." Those descriptions, one suspects, would not qualify in the taxonomic sense as species descriptions—they would, most likely, be descriptions of a few selected characters that one or the other parent possessed in combination.

Chapter 4 (pp. 49-60) is called "Introgression in Finite Populations," wherein essentially a discussion of linkage and genetic drift is presented.

Chapter 5 (pp. 61-80) relates introgression to evolution of organisms, in nature and under domestication.

The sixth chapter (pp. 81-101) surveys the techniques that have been used in studying introgression, largely by Doctor Anderson and his students. He insists on assigning these "various methods of *polygraphic analysis*" formal designations:

1. Scatter Diagrams.
2. Pictorialized Scatter Diagrams.
3. Ideographs.
4. Hybrid Indices.
5. Radiate Indicators.
6. Standardized Photographs.

Illustrations and references to the uses of these several techniques are made throughout the book.

Page 102 constitutes "Epilogue": "How important is introgressive hybridization? I do not know. One point seems fairly certain: its importance is paradoxical. The more imperceptible introgression becomes, the greater is its biological significance." Reason testifies to the truth of that. Yet experience brings exceptions. For example. Along the Rio Negro in Amazonas one may send a boy up a tree in an *estrada* of *Hevea Benthamiana* to lop off a branch. When it crashes to the ground, one sometimes discovers that the branch bears fruit showing definite genetic effect of *H. microphylla*. Perhaps the tree grows only a few steps from an individual that to all appearances is "pure" *Benthamiana*. The first tree might, because of genes from *microphylla*, produce so little latex as to be avoided by the tapper. Introgression there is readily perceptible and of great biological import. And one can find its influence in many *estradas* and for all the species. Similarly, in southeastern Virginia, where *Quercus virginiana* reaches its northern limit, it is easily evident that this entity has been introgressed by a second species, presumably by *Q. lyrata*. In my opinion introgression has been one of the most significant forces in evolution, at least of plants, and surely in some groups recognition of its effective influence does not require exquisite precision.

This is, therefore, an important book. Few of the ideas are new, but here they are conveniently brought together from various sources. The logic of the presentation will not be contested by those who have seriously thought about gene insertion from one germplasm into another, whether species or greater or lesser categories are concerned. The author has the facility of saying simple things as well as complex ones in so simple a manner that his arguments seem obvious. Moreover, he writes in a catchy manner. These are fortunate abilities. Systematists without understanding of genes and chromosomes should be able to comprehend the basic concept of introgression and to use the techniques that are offered. Wiser interpretations of groups of organisms would eventuate, and fewer names for variants. And likewise some of those individuals who administer plant-breeding programs for combining such complex characters as yield and disease resistance would profit from this book: they would learn to found their approaches on something more substantial than naivete and 1910 genetics. Certainly in time, and partially because of such writings as Anderson's, it is to be reasonably expected that most biologists will come to accept the fact that natural hybrids occur and can be recognized for what they are.

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